JOURNAL

OF THE

WASHINGTON ACADEMY OF SCIENCES

VOLUME 35 NOVEMBER 15, 1945 No. 11

BIOLOGY.—*Suggested terms for the interpretation of speciation phenomena.*[1]

S. DILLON RIPLEY, U. S. National Museum. (Communicated by HERBERT FRIEDMANN.)

In the present state of systematic usage, there is a well-established tendency to revise nomenclature in order to fit in with the new concepts emanating from the laboratory and the field. However, the multitude of speciation phenomena emerging from these studies makes a simple trinomial system seem totally inadequate. Huxley's suggestion (1942, p. 410) about subsidiary terminologies which can be introduced to define "the cytogenetic and ecological data of systematics, and the facts concerning actual or potential interfertility," while still not interfering with the taxonomic convenience of the main terminology, seems a very wise one. A brief discussion of some of these terms follows here, with particular reference to current usage in ornithology. I am grateful to Dr. Herbert Friedmann for several valuable suggestions.

GENUS

The genus as a taxonomic term still lacks reality in genetic expression. We accept it as a valid category, however, realizing that it has reality in nature. The genus is being affected at the present time by speciation work on species problems. Wherever possible species are being combined and reduced in number. As a reflection of this, genera tend to follow suit. Generic names are being used nowadays to express degrees of relationship, a reversion to the Linnaean concept, rather than to express degrees of difference. The introduction of subspecies enables the species category to absorb part of the function previously held by the genus. As well as this the better understanding of the genetic basis for morphological differences tends to reduce the degree of importance formerly attached to obvious structural characters. As species become polytypic, so genera become increasingly polytypic in taxonomic usage, in order to maintain proportion. In ornithology the process of "tidying up" the arrangement of the genera of birds is now proceeding apace.

A definition of the genus as presently understood by speciation-minded ornithologists might read somewhat as follows: a natural catch basket which can be determined on morphological criteria but which so far eludes precise genetic analysis. This catch basket includes a group of species occupying different stages of relationship each to the other, but still apparently akin.

SUBGENUS

In the increasing cases where genera contain a large number of species some effort is usually made, by systematists of every hue, to provide subdivisions, higher than the species level, to define groups of species. Many systematists favor the use of a subgenus category. This is an orthodox category and should be adhered to if possible for convenience's sake. But what does it mean? Ridgway (1886) defines a subgenus as "a subdivision of a genus, of indefinite value, and frequently not recognized by name except in the grouping of species." In other words a subgenus can mean pretty much anything at all. If an author then is to use the term he should specifically define his use of it.

Mayr (1942, p. 290) suggests that subgenus if used in combination with genus, species, and subspecies amounts practically to

[1] Received June 5, 1945.

a quadrinomial system as well as burdening the memory with an extra name to be remembered. He adds that the subgenus is used in ornithology either when an author does not quite dare to create a new genus in the face of growing opposition to such a procedure, or when he does not quite dare to sink an old well-established and well-known generic name. Another comment by Dunn (1943) is that since subgeneric names are indistinguishable from generic ones, there is a tendency for later authors to elevate them to generic rank. These remarks are possibly somewhat facetious, but they emphasize one aspect of the problem, that of the difficulty of the personal equation in authors. It is certainly true that the grouping of species into subgenera with their attendant lists of morphologic criteria, often irrelevant in plastic groups, seems a somewhat static way to list cognate species which are undergoing a dynamic process. I would urge then that plain subgenera not be used unless the particular category to which they belong is strictly defined.

OTHER TERMS

Several terms have arisen recently, some as a result of earlier theoretical work, for example, Kleinschmidt's "Formenkreis" carried further by Rensch, others in response to experimental evidence. Most of these terms are concerned with defining a natural monophyletic group lying somewhere between a species and a genus. Starting with that category most closely approaching the genus and listing them in descending order toward a straight species, we have the following:

(1) *Cenospecies.* Clausen, Keck, and Hiesey (1939) have tried hybridizing many plants belonging to the Compositae. They define cenospecies as those groups of species in which there is an absolute genetic barrier, although the ranges are similar or overlapping. This condition has not been well examined in animals except in *Drosophila* and may not be particularly common. Most closely related animal species seem to be able to produce viable and presumably reproducing hybrids, at least under artificial conditions.

(2) *Interspecies.*[2] I propose the use of the term *interspecies* to define a species group or sympatric subgenus, containing *a closely related group of geographically overlapping species which have attained physiological isolation in nature.* Such species may be monotypic or not. It does not affect the definition whether the species overlap only on the margins of their respective ranges, or whether one species is contained wholly within the range of another, i.e., double invasions of islands. This condition has previously been designated informally as a species group (Dice, 1940) for the deer mice, *Peromyscus*, where two species *leucopus* and *gossypinus* live side by side in part of their range without interbreeding although interfertile in the laboratory. Birckhead and myself (1942) used the term to describe the fruit pigeons of the *Ptilinopus purpuratus* assemblage on the Pacific islands. Similarly Mayr and myself (1941) used species group in discussing the Polynesian triller, *Lalage*, wherein two cases occurred of sympatric species obviously most closely related to each other. Diver (1940) discusses several such cases among plants, invertebrates, and insects. In the great majority of cases, it is at present impossible to prove whether two closely related animal species may be cenospecies or interspecies but this in no way invalidates the theory behind the terms. I can not think of two closely related bird species ever having been proved intersterile.

(3) *Superspecies.* Mayr (1931, p. 2) has proposed the term superspecies (instead of Rensch's "Artenkreis") for a systematic unit containing geographically representative species that have developed characters too distinct to permit the birds to be regarded as subspecies. This term symbolizes the next step but one above a simple polytypic species, containing units which have attained a degree of morphological difference implying reproductive isolation. I feel that Huxley (1942, pp. 179, 407) has confused the terminology somewhat by defining "Artenkreis" as equal to a geographical subgenus and restricting the use of superspecies (or supraspecies as it is sometimes mistakenly called) to intermediate situations in which the majority of forms of a

[2] *Inter-species*, species living among each other.

"Kreis" of allopatric groups are clearly subspecies of a polytypic species; "but a few have diverged further until they are probably or certainly regarded as separate monotypic species." This all seems to be an unnecessary complication, the necessity for which is eliminated by Mayr's amplification of his superspecies definition (1942, p. 169), to include both monotypic and polytypic members which are allopatric and are members of a monophyletic group. Thus geographical subgenus, allopatric subgenus, supraspecies, and the two terms of Clausen, Keck, and Hiesey (l.c.) for examples in plants, namely ecospecies and species complex, may be considered as names for a similar phenomenon as that expressed by superspecies. In the case of the last two terms, the difference between them is whether the species concerned show relative or absolute intersterility. As in the case of cenospecies this is a criterion which has not been proved to apply in the majority of closely related animal species.

Possible mechanisms for the successful maintenance of interspecies in contrast to simple geographical isolation in the case of superspecies have been suggested by several authors. Lack (1941) points out that habitat preferences may serve as a barrier once forms have remet after speciation has occurred. Diver (l.c.) concludes that as complete overlap in an ecological sense is presumably hardly ever present, "drift" or random differentiation in small partially isolated populations may be responsible. Actual psychological or physiological mating barriers are discussed by Dice (l.c.) and Diver (l.c., p. 326). Their relative importance in order to produce drift phenomena is probably great. Muller (1940) indicates the importance of isolation, even in partial degree, in producing effects of reduced fertility and viability after crossing.

The development of such a process is suggested by Huxley (l.c., p. 251) to be occurring among the grackles (*Quiscalus*) where a zone of hybridization between two subspecies increases steadily in area from southwest to northeast. This has a parallel in time, for the original hybridization must have occurred in the southwest and has spread to the northeast. Huxley suggests that the restriction of the hybrid zone at the original point of contact indicates a developing stabilization of the condition of selective disadvantage of the hybrid form. This may eventually be carried to the final stage of elimination of interbreeding, leading to the formation of an interspecies.

With the greater degree of speciation study now being applied in systematic groups, it seems likely that there will be an increasing discovery of cases of partially sympatric or even totally sympatric forms which for one reason or another have succeeded in evolving in spite of being most closely related to each other. It is likely also that in the world of the future with the breaking down, principally by the agency of man, of ecological barriers, more and more species will be thrown in direct contact with each other which previously were spatially isolated. An example of this occurs today on the island of Ceylon, where the extensive foresting and the wide spread of tea plantations with the development of new biotic conditions have disrupted the ranges of many species. Two closely related forms of the genera *Dicrurus* and *Gracula*, which Whistler (1944) calls in each case subspecies believing that they occur in separate ecological zones, have been found by me to occur in the same area without evidence of interbreeding. This is apparently a recent development as Whistler was depending on the early literature for his evidence rather than on newly collected material.

As classification and arrangement of forms in check lists, generic revisions, etc., proceed, it seems important to attain some method of indicating relationships. Some recent authors in ornithology (e.g., Mayr, 1941, and Delacour and Mayr, 1945) have introduced the superspecies concept into formal taxonomic lists. I feel that this procedure is welcome, but that in view of the present state of our knowledge it does not go far enough. It is obvious that geographical isolation is the cornerstone of much of the speciation process, but it is also obvious that physiological isolation as postulated by Dobzhansky (1940) is in many cases a subsequent development which can result in allowing closely related species to live side by side. Thus to list only superspecies is to fail to give the complete picture of relationship. As an example, Mayr (1941, pp. 91–92) lists several species of kingfisher, including *Tanysiptera hydrocharis* and *T. galatea*. *T. galatea* is combined with several other species into a superspecies, but *T. hydrocharis* is left out because its range overlaps with *T. galatea* in southern New Guinea. Actually *T. hydrocharis* is most closely related to the latter species but has succeeded in attaining physiological isolation allowing it to live in the same area without hybridizing. Another example is the group of kingfisher species, *Halcyon chloris, sancta, cinnamomina, saurophaga, veneratus*, etc., figured by Mayr (1942, p. 181). Several examples in Delacour and Mayr's revision of the duck family (l.c., pp. 37–42) are also pertinent. Thus in the large genus *Dendrocygna, javanica, bicolor*, and *arcuata* are all intimately related, but *bicolor* and *arcuata* alone are bracketed as a superspecies. In the genus *Anas*, *bernieri* and *gibberifrons* are listed as one superspecies, *castanea* and *aucklandica* as another. And yet *castanea* and *gibberifrons* are so closely related from the morphological and distributional evidence available that were it not for an apparent overlap in their ranges they would be included as races of the same species. These two forms hybridize easily in captivity but apparently not in nature. Finally, in the genus *Aythya* the three species *valisneria, ferina*, and *americana* are all obviously of close relationship. However, geographical overlap prevents their being bracketed as a superspecies. In these cases I would include all the species in one interpsecies.

(4) *Emergent interspecies*. By this term I would define a species group containing a closely related group of geographically overlapping species with a marginal fringe of hybridization. Such a species group would normally include forms, one member of which at least tends to break up into geographical subspecies. Examples of this condition in birds are the woodpeckers *Colaptes auratus* and *cafer* (Huxley, l.c., p. 250), the crows *Corvus corone* and *cornix* (Meise, 1928), and the kingfishers *Ceyx erithacus* and *rufidorsus* (Ripley, 1942). Similar phenomena have been indicated among mammals (Banks, 1929, and Dice, l.c.), reptiles (Stull, 1940), fishes (Hubbs *et al.*, 1943), and insects (Carothers, 1941; Sweadner, 1937).

A special group of emergent interspecies are the cases where the terminal links in a chain of species or subspecies meet. A classic case is that of the gulls, *Larus argentatus* and "*fuscus*" figured by Mayr (1942, p. 180). Apparently there is a certain amount of interbreeding between the terminal links (vide Huxley l.c., p. 244). Another variation occurs in the creepers *Certhia familiaris* and *brachydactyla*, which behave like an interspecies except in the Caucasus where hybridization occurs. A further case of this sort occurs in the tits *Parus major* and *minor* as described by Rensch (1933), where hybridization occurs at certain zones of overlap, not at others.

Possibly the term semispecies of Mayr (1940) could be used to characterize cases such as those listed above. However, as defined by Mayr hybridization was not a criterion. Rather he used it to denote forms which "can be deduced to be geographical representatives of some other species, but have during isolation developed morphological differences of the order of magnitude to be seen between undoubted species." I believe that it would have been far more satisfactory to have defined semispecies with regard to the degree of interfertility rather than with regard to morphological difference by degree. Every taxonomist will have his own standard of degrees of morphological difference as between the category species or subspecies. Semispecies has thus been defined on the basis of a sliding scale.

SPECIES AND SUBSPECIES

Below these categories are species and subspecies which have been frequently and well defined in recent times. However, round the margins of species and subspecies hover cases which seem to be *in statu nascendi*. An example of a species in which two waves have met and hybridized so completely in nature that only one species can be considered is *Pachycephala pectoralis* in the Solomon and Fiji Islands (Mayr, Amer. Mus. Novit. nos. 522, 531. 1932). This species contains two color forms: (a) with yellow underparts and (b) with white throat, which apparently represent two closely related waves of immigrants. If these waves had not been coextensive, but had remained representative, they would have been considered two well-marked species forming a superspecies. If, on the other hand, some of these forms had been discovered on the same islands without (due to the vagaries of field collecting) any evidence of hybridization, then there would have been no recourse but to consider them an interspecies. A small degree of interbreeding on the fringe of their ranges would have indicated a terminal condition serving to define the forms as an emergent interspecies. In this case, however, hybrizidation is too complete. Hybrid populations have been named and the apparent phenotypic differences have been proved to have little if any genotypic parallel. A somewhat similar example is found in the juncos (Miller, 1941).

It is to be hoped that all cases of this sort will in the future be fully discussed by biologists in order to emphasize the importance of studying these phenomena, both by laboratory and field workers. Only in this way will it be possible to define the speciation process.

SUMMARY

A number of terms are discussed by which various types of speciation may be described. It is suggested that these terms be used as an auxiliary to the main nomenclature of genus, species, and subspecies. It is further suggested that all evidence of unusual cases of speciation phenomena be pointed out and described by scientific writers in order to widen and extend the literature, and thus promote further study.

LITERATURE CITED

Banks, E. *Interbreeding among some Bornean leaf-monkeys of the genus* Pithecus. Proc. Zool. Soc. Loncon 1929: 693.

Carothers, E. E. *Interspecific grasshopper hybrids.* Proc. VII Int. Genet. Congr. (Edinburgh, 1939): 84. 1941.

Clausen, Jens, Keck, D. D., and Hiesey, W. M. *The concept of species based on experiment.* Amer. Journ. Bot. **26**: 103. 1939.

Delacour, J., and Mayr, E. *The family Anatidae.* Wilson Bull. **57** (1): 3. March 1945.

Dice, Lee R. *Speciation in* Peromyscus. Amer. Nat. **74**: 289. 1940.

Diver, C. *The problem of closely related species living in the same area.* "The New Systematics": 303. Oxford, 1940.

Dobzhansky, T. *Speciation as a stage in evolutionary divergence.* Amer. Nat. **74**: 312. 1940.

Dunn, E. R. *Lower categories in herpetology.* Ann. New York Acad. Sci. **44**: 131. 1943.

Hubbs, C. L., Hubbs, L. C., and Johnson, R. E. *Hybridization in nature between species of catostomid fishes.* Contr. Lab. Vert. Biol. Univ. Michigan no. 22. July, 1943.

Huxley, J. *Evolution, the modern synthesis.* New York, 1942.

Lack, D. *Some aspects of instinctive behavior and display in birds.* Ibis 1941: 407.

Mayr, E. *Notes on* Halcyon chloris *and some of its subspecies.* Amer. Mus. Novit. no. 469. 1931.

———. *Speciation phenomena in birds.* Amer. Nat. **74**: 249. 1940.

———. *List of New Guinea birds.* American Museum of Natural History, New York. 1941.

———. *Systematics and the origin of species.* Columbia Univ. Press. 1942.

Mayr, E., and Ripley, S. D. *Notes on the genus* Lalage *Boie.* Amer. Mus. Novit. no. 1116. 1941.

Meise, W. *Die Verbreitung der Aaskrähe* (*Formenkreis* Corvus corone *L.*). Journ. für Orn. **76**. 1928.

Miller, A. H. *Speciation in the genus* Junco. Univ. California Publ. Zool. **44**, no. 3. 1941.

Muller, H. J. *Bearings of the* Drosophila *work on systematics.* "The New Systematics": 185. Oxford, 1940.

Rensch, B. *Zoologische Systematik und Artbildungsproblem.* Verh. Deutsch. Zool. Ges. 1933: 19.

Ridgway, R. *A nomenclature of colors for naturalists, and compendium of useful knowledge for ornithologists.* Boston, 1886.

Ripley, S. D. *A revision of the kingfishers,* Ceyx erithacus *and* rufidorsus. Zoologica **27** (2): 55. 1942.

Ripley, S. D., and Birckhead, H. *On the fruit pigeons of the* Ptilinopus purpuratus *group.* Amer. Mus. Novit. no. 1192. 1942.

Stull, O. G. *Variations and relationships in the snakes of the genus* Pituophis. U. S. Nat. Mus. Bull. **175**. 1940.

Sweadner, W. R. *Hybridization and the phylogeny of the genus* Platysamia. Ann. Carnegie Mus. **25**: 163. 1937.

Whistler, H. *The avifaunal survey of Ceylon.* Spolia Zeylanica **23** (pts. 3 and 4): 119. 1944.